Subterranean Biology 46: 165–198 (2023)
doi: 10.3897/subtbiol.46.114190
https://subtbiol.pensoft.net

IN MEMORIAM

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

The biospeleological work of Carl L. Hubbs (1894–1979): an appraisal

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Academic editor: Fabio Stoch | Received 14 October 2023 | Accepted 8 November 2023 | Published 22 November 2023

https://zoobank.org/956147F3-E719-453A-8B01-A57A455A3893

Citation: Romero Jr. A, Moseley M (2023) The biospeleological work of Carl L. Hubbs (1894–1979): an appraisal. Subterranean Biology 46: 165–198. https://doi.org/10.3897/subtbiol.46.114190

Abstract
Carl Leavitt Hubbs (1894–1979) was a prominent and internationally renowned American ichthyologist whose publications include taxonomic descriptions of several North American blindfishes including the Mexican Cave Characin. His archived personal papers reveal a wide-ranging interest in the biology and evolutionary origins of cave and blindfishes, and his discussions and disputes with colleagues about their taxonomy. He also took opportunities to collect other fauna from American caves during the inter-war decades. Drawing upon his unpublished archive and other relevant sources his biospeleological work is chronicled in detail and discussed in the context of his other work.

Keywords
Carl L. Hubbs, Cavefishes, Biological Species Concept, Biospeleology

> "*For the arriving at the inside of things, the publication of letters is the true method.*"
> - Cardinal Newman

Introduction

Carl Leavitt Hubbs (1894–1979) was one of the twentieth century's most prolific and respected American biologists. He was a prominent and internationally renowned ichthyologist, mainly interested in the systematics and distribution of freshwater fishes of

North and Central America and Pacific marine fishes. His first published paper, which was on Japanese flatfishes, was a classical taxonomic work (Hubbs 1915) and the taxonomy of fishes always remained a central component of his work.

Nevertheless, although known mainly as an ichthyologist his involvement in natural history went much wider. He always retained a broad range of interests: Norris (1974) describes him as a "*modern pioneer naturalist*". His eclectic bibliographic output includes works on marine mammals, ornithology, paleontology, archaeology, zoogeography, climatology, evolution, ecology, and the history of science. He was also involved in conservation and applied fisheries research. From 1915 until he died in 1979 he authored or co-authored more than seven hundred publications and received several prestigious academic awards, including election to the U.S. National Academy of Science in 1952.

Within this copious output of published work, a handful of papers are devoted to blind fishes of hypogean (cave, artesian) freshwater habitats and certain morphologically similar marine species (Hubbs 1926, 1927, 1936, 1938; Hubbs and Innes 1936; Hubbs and Bailey 1947). To biospeleologists it is as the author of these works that his name is most likely to be familiar. Primarily they are descriptions of new taxa (Table 1) but also include conjectural discussions on the evolution and ecology of these animals.

However, his archived personal papers show that his published contributions on blind fishes only partly reflect the full scope of his interest in the topic. He recognized reduction and/or disappearance of eyes in fishes as a widespread phenomenon occurring in some deep-sea species and those inhabiting burrows and silty waters, as well as the subterranean forms. Throughout his career he speculated about the ecology and evolutionary origins of blind fishes, and collected notes and references with the intention of writing a monograph on them. He also became interested in cave fauna other than fishes, whenever he could taking the opportunity to collect invertebrates from caves in the continental USA.

Despite his acknowledged contributions to biospeleology, his overall work in this area has never been highlighted or discussed in depth, either by himself or by others. He was never able to complete the treatise on blind fishes or, for that matter, on evolution and speciation, topics that became a focus throughout much his career. Interestingly he himself said the same of Joseph Grinnell: "*To the end of his days* [he] *kept too busy with special researches to … write books which would bring together and make generally available his highly respected views on the relations between organisms and their environment*" (1943b, p. 466).

Table 1. Cave and other blind fishes described by Hubbs.

Name given by Hubbs and publication date	Current name
Lethops connectens Hubbs, 1926	Still valid
Anoptichthys jordani Hubbs & Innes, 1936	*Astyanax fasciatus* (Cuvier 1819)
Typhliasina pearsei Hubbs, 1938	*Ogilbia pearsei* (Hubbs 1938)
Pluto infernalis Hubbs, 1938	*Ophisternon infernale* (Hubbs 1938)
Satan eurystomus Hubbs & Bailey, 1947	Still valid

Fortunately for historians of science Hubbs donated his papers, including correspondence and notes, to the library of the University of California in San Diego (UCSD) [https://library.ucsd.edu/speccoll/findingaids/smc0005.html]. These include documents from his time at the University of Michigan (1920–1944) and those from his time at the Scripps Institution of Oceanography (1944–1979) at UCSD (Fig. 1).

Drawing upon this extensive unpublished personal archive, his published works, and relevant secondary sources, we document and review his thinking on blind fishes and cave fauna, most of which has never been treated in the literature.

Methods

As primary sources, we examined all the records kept at UCSD. We selected and ordered copies of all that relate directly to biospeleology, totaling 668 documents. We paid particular attention to those dealing with blind fishes described by Hubbs. The selected documents were organized and analyzed according to the sender and the recipient(s), date on which they were written, and the kind of document (letters, cards, handwritten notes, telegrams, newspaper clippings). We also reviewed all Hubbs' original publications on this matter. Museum collection specimen accession data and

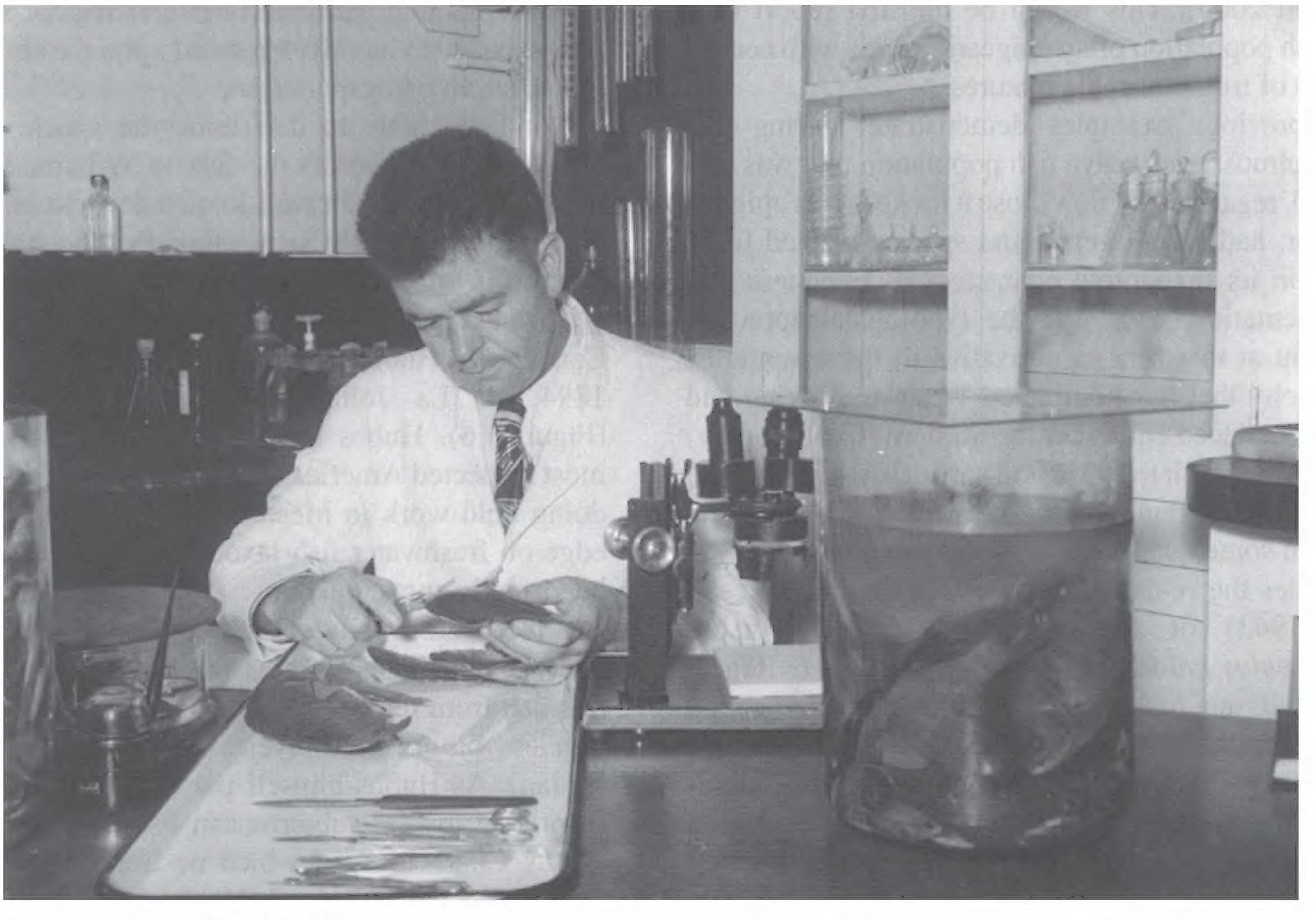

Figure 1. Carl Leavitt Hubbs in his laboratory at the Scripps Institution of Oceanography. This picture was taken in 1945, shortly after he had made his major contributions to hypogean fish research (Photograph courtesy of the Scripps Institution of Oceanography Library).

references in specialist taxonomic works to material collected by Hubbs provided some additional details.

In the following the archived documents are cited by their Group and Box location in the UCSD archives, abbreviated as for example G14B028.

Biographical background

Hubbs was born in Williams, Arizona, on October 19, 1894, moving with his mother to California when still an infant. While living in Los Angeles, an ichthyologist and Junior College teacher, George Bliss Culver (1875–1949), encouraged him to study fishes and advised going to Stanford University, which at the time had become the pre-eminent center of American ichthyology under the leadership of David Starr Jordan (1851–1931). He registered at Stanford in 1913 (Norris 1974, p. 587; Miller and Shor 1997, p. 367).

After completing his B.A. (1916) and M.A. (1917) degrees at Stanford, Hubbs was employed briefly (1917–1919) at Chicago's Field Museum of Natural History (FMNH) as an Assistant Curator. In 1919 he moved (apparently actively recruited) to a curatorial position at the University of Michigan Zoology Museum (UMZM). He was to remain at Michigan for the next twenty-five years, in 1924 taking over the Division of Fishes created in 1920 under the leadership of Walter N. Koelz (1895–1989). He was awarded a doctorate in 1927 on the basis of a paper already in press and overall publication record, and a full professorship in 1940.

Hubbs' next and final career move was to Scripps Institute of Oceanography in October 1944. He died at La Jolla, California, on June 30, 1979.

Fuller accounts of Hubbs' life and career are provided by Norris (1974), Horn (1976), Shor (1979), Shor et al. (1987) and Miller and Shor (1997). Norris (1974) is a particularly sympathetic presentation given on the occasion of Hubbs' eightieth birthday. It is accompanied by a list of Hubbs' doctoral students compiled by his wife Laura (Hubbs 1974) and an extensive selected bibliography (Shor 1974). For a comprehensive indexed bibliography of his published work see Miller (1981).

First encounters with blind fishes

The quarter century that Hubbs worked at Michigan was the period that gave him the most opportunities to study blind fishes. Being inland, the State was an appropriate base for investigating the continental freshwater fish fauna. In addition, it was well situated geographically for travel to the limestone karst regions of Indiana and nearby states. After 1944 when he moved to Scripps Institute, his obligations and focus shifted to the Pacific marine fauna. It is thus perhaps ironic that his first encounter with blind fishes, and first speculations about their evolutionary origins, was not with subterranean forms but with certain marine species endemic to the Pacific coasts of the United States and Mexico.

This first field encounter of a blind fish was with the California Blind Goby (*Typhlogobius californiensis* Steindachner, 1879), a small species ("*circa*" 8 cm) that when adult is a specialized commensal sharing the burrows of a marine crustacean *Neotrypaea biffari* (formerly known as *Callianassa* sp.). It is one of a varied fauna of gobioid fishes found in the littoral and shallow sub-littoral of tidal flats and sandy or muddy bays in California. *Typhlogobius* adults lack eyes and dermal pigmentation: convergent morphological features that it has in common with many cavefishes (Eigenmann 1909 pp. 65–69). The free-swimming juveniles retain rudimentary eyes which is another trait commonly seen in cavefishes (Romero and Green 2005).

It is possible that Hubbs knew of the California Blind Goby from his early years when he was living in coastal California, and even if not, he must have read of it in the work of Carl H. Eigenmann (1863–1927) (Romero 1986b). He presumably became aware of Eigenmann's work on blind vertebrates during his student days at Stanford and was undoubtedly familiar with his publications by the early 1920s. The earliest documented evidence of him searching for a blind fish is a collecting trip to the California coast with his wife Laura in 1922.

In December of that year, the couple collected a single specimen of a previously unknown species that lives in kelp forests but phenotypically is intermediate between *Typhlogobius* and more typical, fully eyed, gobies. The Halfblind Goby (*Lethops connectens* Hubbs, 1926) was described from the type specimen (UMZM Accession no. 63281) and two paratypes (UMZM 63282) that Hubbs collected in May of the following year (Hubbs 1926). The eyes remain functional but become almost rudimentary in the adult, and, while chromatophores remain, no color pattern is evident. Tactile organs are well developed, and scales are absent.

This discovery appears to have been the initial spur of his lifelong interest in the phenomenon of eyelessness in fishes in general including subterranean forms, those inhabiting burrows, silty waters of tropical rivers and estuaries, and deep-sea species. In the year following his description of *Lethops* he published a second paper in which he speculated about the evolutionary origins of this and *Typhlogobius*, drawing a parallel with the North American fish family Amblyopsidae (Hubbs 1927). It was also, in 1924, not long after discovery of *Lethops* that he began investigating cave-associated fishes, collecting amblyopsids in Indiana caves.

The Amblyopsidae

In the mid-1920s the only blind subterranean blind fishes know to occur in North America were amblyopsid cave fishes and a catfish recently described from artesian wells in Texas (*Trogloglanis pattersoni* C. H. Eigenmann, 1919). Amblyopsidae is a small freshwater family (Order Percopsiformes: Trout-perches) distributed in the southern and eastern (unglaciated) United States. The systematics of the family is in flux. Traditional taxonomy relying on gross morphological traits (which result mostly from convergent evolution) has been proven to be unreliable: modern genetic studies

have shown that these fishes are much more taxonomically complex than previously believed (Romero 2004).

As currently envisaged, Amblyopsidae is represented by six genera and nine species. Most of the recognized species are exclusively subterranean (stygobites), lacking superficial pigmentation and with eyes reduced or absent. The family exhibits a transitional series from the surface (epigean) Swampfish (*Chologaster cornuta*); the Spring Cavefishes (*Forbesichthys*) which are facultative cavernicoles (stygophiles) inhabiting both springs and caves; and finally obligate cavefishes (*Amblyopsis*, *Speoplatyrhinus*, *Troglichthys*, *Typhlichthys* (Eigenmann 1909; Romero 2004; Adams et al. 2019).

The eyes of amblyopsids range from small (microphthalmic) in the epigean and stygophilic species, to vestigial (remnant eye tissue under the skin) in those living permanently underground (stygobitic). Stygobitic species are also characterized by: (l) depigmentation (they have a pinkish color due to the blood vessels showing through the translucent skin, with only a few, mostly nonfunctional, melanophores); (2) low metabolism; (3) low fecundity; and (4) increased swimming efficiency, tactile receptivity, and longevity.

Cave fieldwork at Michigan 1924

Hubbs' correspondence archive before 1936 is not very informative about the present topic, presumably because his relevant activities, being based in Michigan, rarely involved a need to communicate with workers elsewhere. From 1924 to 1935, his activity has been reconstructed from a few extant field reports, museum accession data, occasional comments in later letters, some surviving correspondence 1931–1935, and published papers.

We do know that in the spring of 1924 he led a small party on a trip to Indiana to collect amblyopsids on behalf of UMZM. They investigated several caves in the limestone district of southern Indiana from the 15th to the 18th of May. Indiana was reasonably accessible by road from Michigan in the 1920s, and several caves in the southern limestone district were already well-known and not difficult to reach and explore. In addition, they already included recorded localities for what was at the time identified as the most common cavefish, *Amblyopsis spelaeus*. Wyandotte Cave is one of the two original localities (the other being Mammoth Cave, Kentucky), and the species had also been recorded in another Indiana cave, Rhoad's Cave (Banta 1907, p. 23; Eigenmann 1909, p. 71). The Indiana population of *Amblyopsis* has been separated recently from *A. spelaea* as *A. hooseri* (Adams et al. 2019).

Handwritten accounts of this collecting trip are preserved in the Hubbs Archives. The most informative is a series of short unsigned reports detailing individual caves visited (G16B028).

There is no full record of the party members. Further details (including UMZM Accession Numbers) of the fishes collected and the caves can be found in Hubbs' notes in archive file G26B29 and Table 2 herein.The party explored the main, higher level of Marengo Cave on the 15th, finding pools but no flowing water. Just before midnight on the 15th, they reconnoitered the lower active stream passage ("Old Town Spring

Table 2. Hypogean fishes collected by Hubbs.

Date	Location	Description	Taxon	Explorers	Specimen	Notes
16.5.1924	Siberts Well Cave, Indiana	Active stream cave in limestone. c. 3ft deep, between pools	*Amblyopsis spelaeus* (Amblyopsidae)	CLH & A.C.Kennedy	UMZM 64997	Near Wyandotte Cave. Also 1 *Eurycea* salamander
16.5.1924	Old Town Spring Cave, Marengo Cave, Indiana	Active stream cave in limestone. Large pools well inside 'long dark cave'	*Cottus bardii carolinae* (Cottidae)	CLH & party	UMZM 54998	Some 'huge'. Living in cave. No eggs or young seen.
16.5.1924	Old Town Spring Cave, Marengo Cave, Indiana	Active stream cave in limestone. Large pools well inside 'long dark cave'	*Semotilus a. atromaculatus* (Cyprinidae)	CLH & party	UMZM 64999	Blind *Cambarus* in pool
16.5.1924	Rhodes Farm cave nr. Croydon , Indiana	Limestone cave. Deep pool, c. 150' from entrance, no current, "thoroughly dark"	*Hyborhynchus notatus* (Cyprinidae)	CLH & E. B. Williamson	CLH, UMZM 64996	Described as a half-grown straggler minnow
17.5.1924	Twin Caves, nr. Mitchell, Indiana	Active stream cave in limestone. Pools in stream, no current	*Amblyopsis spelaeus* (Amblyopsidae)	CLH & party	UMZM 65000	
19.8.1930	River Cave, Campden County, Missouri	Large, deep (<10') clear pools	*Typhlichthys* sp. (Amblyopsidae)	CLH ?	UMZM 156795, UMZM 156796	Associated with pale crayfish *Cambarus* sp. and blind salamamders.
19.8.1930	unnamed cave, Campden County, Missouri	Small limestone cave with fast-flowing stream. Stream, mud bottom	*Cottus williamsoni* (Cottidae)	CLH?	UMZM 102747	
24.9.1931	Jewel Cave, Dickson Co.	Active stream cave in limestone. Pools, mud & lmst bottom, no current, `13.5 C.	*Chologaster agassizii* (Amblyopsidae)	CLH	UMZM 97211	CLH refers to it as *Forbesichthys agassizii*: (CLH to Leslie Hubricht 29th October 1942)

Cave"), entering it for a short distance. Returning early the following morning, they successfully followed it to the end. The same day they visited another active stream cave, "Siberts Well Cave" (the stream outlet of the famous Wyandotte Caverns system) and Rhoad's Cave. The latter consists of a steeply descending passage ending at a deep sump pool. Mitchell Caves and Twin Caves, other parts of the Wyandotte system, were examined on the 17th and the 18th.

It is reasonable to assume that obtaining examples of *Amblyopsis* was the main purpose of the trip. Specimens were secured in Sibert's Well Cave and Twin Caves. He also made observations on and collected specimens of all other fishes seen underground. At least two common epigean species of minnow (Cyprinidae) were present: *Semotilus atromaculatus* in "Old Town Spring Cave" and *Hyborhynchus notatus* in Rhoad's Cave. Both were taken in lightless regions, but Hubbs thought neither to be resident there. Several sculpins (*Cottus bardii carolinae*) including some exceptionally large individuals were living deep inside "Old Town Spring Cave", evidently permanently although no eggs or young were seen. They had been feeding on cavernicolous crayfish. He speculated that the large size reached by these cave-dwelling sculpin (confirmation of a phenomenon previously reported in Indiana cave populations by

Hay [1894]) was due to the protection from predators offered by this habitat. Banta (1907, p. 75) had previously suggested this explanation for the relatively large size attained in Indiana caves by the epigean crayfish *Cambarus bartoni* and the amphipod *Crangonyx gracilis*.

Hubbs may have recalled this example three decades later when interpreting another cyprinid (*Hesperoleucus symmetricus*) that had been collected in Bower Cave, Maripoan County, California and found to be a very old individual (see below).

The notes include observations of the presence of other cave fauna: frogs (*Rana* sp.), salamanders (*Eurycea* sp.), crayfish (*Cambarus* sp.), and various other, unidentified, invertebrates. This is early evidence of Hubbs beginning to take a wider interest in cave fauna in general. By November of 1924 accompanied by a Dr. Jan Metzelar, he was again searching for cave fauna, this time in a small Ohio cave. Evidently, the results were disappointing and all they secured were a few overwintering bats identified as two common species *Pipistrellus s. subflavus* and *Myotis subulatus*.

Hubbs was an inveterate collector amassing huge fish collections at UMZM and later at Scripps (Miller and Shor 1997) and this might well be sufficient to explain why he paid attention to and collected specimens of anything seen, not only the blind cavefishes. However there is significance for his later conjectures in that he approached the animals occurring in caves with the broad viewpoint of a naturalist. He was not constrained in his thinking by a purblind belief commonplace in biospeleology that blind, depigmented animals are the only animals that really matter (or even belong) in subterranean habitats – the only "true" cavernicoles. The focus on these species at the expense of the many other animals that are to be found in subterranean habitats has been termed, admittedly not very elegantly, "troglocentrism" by one of us (Moseley 2007, pp. 1, 11). Rarely made explicit – Weber (2000) is an exception – it nevertheless underlies and pervades the biospeleological literature. This has had some negative implications for the sub-discipline. Romero (2009) noted that this phenomenon may be due at least in part to the fact that it is usual for cave biologists (including the present authors) to have started out as active cavers, hence naturally tending to approach the subject from a 'cave-centered' perspective. Hubbs in contrast should not be considered to be a "caver". He was about 30 years old in 1924 which would have been late in life for a caving enthusiast to begin. Certainly, he focussed his attention on those blind animals that everyone at the time saw as "cave animals" but unusually he also observed and noted that some normally surface fish species appeared to derive benefits from living inside caves.

Discussions of troglocentrism can be found in Romero (2009, Chapter 4) and Moseley (2022, p. 40).

Other cave fieldwork at Michigan: 1925–1944

On occasion over the next two decades, Hubbs visited a dozen or more caves, most of them further afield in the South and West of the United States: i.e. Arkansas, Califor-

nia, Indiana, Missouri, Nevada, New York, Ohio, Oregon, Tennessee, Texas, Virginia, and West Virginia (G29B028 CLH to Don Block, NSS; G16B028; G6B028 CLH to W. Halliday 14.12.1948). He was looking for fish but found only known species. He did add a few new occurrence records (a stygobitic amblyopsid *Typhlichthys* sp. and a sculpin *Cottus williamsoni* [an accidental in this habitat?] in Missouri; and the stygophilic Spring Cavefish *Forbesichthys agassizii* in Tennessee) (Table 2).

Reports and rumors of unknown hypogean fishes were assiduously followed up. The earliest is a February 1934 report from a local resident about Bluegill (*Lepornis macrochirus*) seen in a shallow subterranean stream exposed by a surficial collapse a few miles from Grand Rapids, Michigan. Hubbs took the trouble to obtain the area rainfall records in an effort to explain what had happened. It is unclear exactly what he was looking for, but later correspondence suggests that he was thinking that the fishes had dispersed accidentally during a flood event. The outcome is not recorded in the relevant archive (G28B028). This report had been forwarded to him by a colleague, but by 1937 after some newspaper publicity about the Mexican Cave Characin (see below), he was being contacted by informants directly. File G24028 includes an exchange of correspondence concerning a rumor of a blindfish in a cave near St. Paul, Minnesota. Hubbs suspects it to have been a *Cottus* and comments that, although such reports are worth following up, they usually turn out to be blind alleys (8.2.1937 CLH to Prof. King: G24028).

His notes and letters show that he was no longer collecting exclusively to obtain fish specimens for UMZM. Although this remained the primary purpose he realized quickly that little was known about the biology of North American caves. There is a note to this effect in the files (G16B028). The note is undated but undoubtedly comes from this period. Presumably motivated by this, and probably also by simple curiosity ("*I can hardly resist the temptation to go into* [caves] *on passing*" CLH to A. W. Reese 7.3.1933) he also made notes on and collected other vertebrate and invertebrate fauna that he saw in the course of his underground perambulations. These were not methodical surveys: he just secured those obvious, larger animals he saw in a single visit. Nevertheless, this was pioneering work that has been overlooked in the literature: there was almost no other general cave fauna collecting in the United States during the inter-war years. Biospeleology there was "*effectively dead*" (Romero 2009 p. 41). Some specialist taxonomists were certainly interested in receiving and studying cave material but rarely explored caves themselves. For the most part, their work was purely descriptive, confined to occurrence records and reports of new species: one minor exception was a speculative discussion of the evolution of cave isopoda (Miller and Hoy 1939).

It was very different in Europe, where Emil G. Racovitza (1868–1947), René Gabriel Jeannel (1879–1965) and others were engaged in evolutionary theorizing and extensive international surveys of cave fauna (Romero 2009, pp. 50–51). Perhaps reflecting the pre-War isolationist political climate the Americans worked in isolation. The archives show Hubbs corresponding with prominent ichthyologists in Europe and elsewhere but there is no mention of any cave biologist or indication of awareness of their work.

Hubbs had no invertebrate taxonomy expertise, and he did not publish results himself: "*I have done quite a bit of collecting in caves, but .... have published only on*

fishes." (CLH to Edward Danby 22.8.1950: G1B028). His material went off for examination and when appropriate, taxonomic description by specialists. Descriptions and occurrence records are scattered amongst specialist journals and difficult to trace. Several previously unknown subterranean species were obtained including two spiders (*Bathyphantes hubbei* Chamberlin & Wilton, 1943, *Archphantes cavaticus* Chamberlin, 1943); a millipede (*Tidesmus hubbsi* Chamberlin, 1943); a crayfish (*Cambarus hubbsi* Creaser, 1931); an amphipod (*Stygobromus hubbsi* Shoemaker, 1942); and a flatworm (*Kenkia rhynchida* Hyman, 1937 [now *Macrocotyla rhynchida*]).

It was not until the nascent National Speleological Society, founded in 1941, began to inspire biological cave surveys that there was a post-war revival and a more systematic approach in America. File G29B028 shows that Hubbs took an early interest in the fledgling NSS, writing to Don Bloch, then Editor of the Bulletin, on 3.4.1944 requesting information on the society's scope and mentioning having had a longstanding interest in cave fauna. Bloch replied 6.4.1944 enclosing a sample Bulletin and invitation to join, which Hubbs submitted (12.4.1944) with a set of separates of his cavefish publications and an offer to write an article for the Bulletin summarizing his overall cave fauna finds. He received his membership card the following week.

Cavefish taxonomy Michigan 1932–1944

Although by the early 1930s, Hubbs had not yet been able to add significantly to knowledge of the cavefish of the continental USA, he was soon to be gifted an opportunity to study and publish descriptions of exciting new forms that turned up elsewhere in North America: in Mexico's Yucatán Peninsula.

The Yucatán comprises a huge lowland limestone karst region with little topographical relief. Because of the low relief dry (i.e. not flooded) caves are thinly scattered. Most of the freshwater is sub-surface, accessible only in the many flooded sinkholes and shafts known as cenotes that are characteristic of the area. Cenotes typically connect with flooded subterranean passages and conduits. Most Yucatán caves are small but extensive systems with several thousand meters of passages and chambers do exist. Due to the scarcity of epigean waters most of the freshwater fish fauna is found in cenotes or in fully subterranean habitats.

In 1932 UMZM participated in a multidisciplinary expedition to the Yucatán Peninsula led by Professor Arthur Sperry Pearse (1877–1956) of Duke University (Durham, North Carolina). The Carnegie Institution of Washington also participated. This major scientific project generated a series of detailed reports by various experts, with Hubbs responsible for the fishes.

By late 1936 a report on the Yucatán cenotes had been published. Hubbs was unable to report any stygophilic species but *Rhamdia guatemalensis* (Heptapteridae: Four-barbel catfishes) collected from caves by Dr. Edwin Phillip Creaser (1907–1981) (see collection details in G26B29] seemed "*to approach the typical, uncolored, eyeless cave-fishes in their moderate depigmentation and somewhat reduced eyes*" (Hubbs 1936, pp. 166–168, 182–

186). This hint that they are transitional forms is not surprising given his knowledge of the blind gobies and the Amblyopsidae. So, here again (see above), he was clearly aware that it is not necessarily only highly-adapted species that are important in subterranean habitats. This was made explicit in a subsequent paper: "*The not infrequent finding of strays* [sic] *of free-living species in caves shows that caves are very frequently populated with a nucleus from which cave species could theoretically evolve*" (Hubbs 1938, p. 270).

A notorious 'splitter', Hubbs described two cave populations of *R. guatemalensis* as sub-species: *R. g. decolor* (Hubbs 1936, p. 201–203; 1938, pp. 278–280) and *R. g. stygaea* (Hubbs 1936 p. 203–205; 1938, pp. 280–282). Differing from those occurring in the cenotes only in displaying slightly or somewhat reduced eyes and pigmentation, they are unlikely to be anything more than local varieties.

From early June 1936 until August 25th Pearse was back in the Yucatán and now making a specific search for true cavefishes (Hubbs 1938 p. 261; Pearse to CHL 26.8.1936 G27B28). Perceptively he concentrated his effort on caves rather than open-water cenotes. Likely due to the impracticality of exploring physically rigorous deep caves all were small. Of the seven named in Hubbs' later paper the longest (the site where Pearse found the first blind fish) was 260 m (Hubbs 1938). Nevertheless, he was successful.

The strategy of targeting caves was suggested by unconfirmed nineteenth century reports of blind fishes in Yucatán caves, and the 1932 discovery there of stygobiotic crustaceans evidencing the existence of a stygobiotic fauna in the region. It paid off handsomely. On June 8th, probably within days of starting work, Pearse captured a single small blind fish in Balaam Canche Cave, near Chitchén Itzá (Hubbs 1938 p. 291). He must have immediately sent word to Hubbs, who, clearly excited, replied by letter that "*your cryptic news … represents a great rarity*" (CHL to Pearse 18.6.1936 G27B28). The specimen was a juvenile brotulid later designated the paratype of the new species described and initially named as *Typhlias pearsei* Hubbs, 1938 (Table 1).

Pearse also managed to collect a single example of yet another kind of blind cavefish and a second, this time helpfully an adult, specimen of the brotulid. In addition to these were cave-collected examples of a cichlid *Cichlasoma urophthalmus* and more *Rhamdia*. On August 26th after having arrived back home only the previous evening, Pearse sent Hubbs all his material by express mail. In a letter of that same date, he reminded Hubbs that the collecting permit required him to take only three specimens of each species, reserving one for the Mexican national museum: "*Will you please … do what you think is right to fulfill this requirement?*" Hubbs had no intention of giving up the cavefish specimens. His terse reply (16th September) was that "*… we shall proceed to discuss what material we have, with the idea that if we are to lose our collecting privileges thereby, we won't want to continue collecting in Mexico anyway.*" By now, after having had the time to study them he knew that one of the new cavefishes was a brotulid, a normally deep-sea family represented in freshwaters only by two Cuban cavefishes (Romero 2007). The other was an eel of a cosmopolitan family with only one other known cave species (from Africa). "*These blind fishes represent one of the finest ichthyological discoveries in a long time*" (G27B028).

Pearse quickly responded with a short letter requesting a report on these fishes for inclusion in a planned account of the animals of the caves, to which Hubbs readily agreed. Just a week later he asked for guidance where this was to be published so that the UMZM artist could prepare illustrations at the right scale. It took only two days for Pearse to get and forward the information that the Smithsonian had agreed this (G27B028).

Carl Hubbs had been gifted an exclusive opportunity to publish what was, in his own words, "*one of the finest ichthyological discoveries in a long time*"; to which he himself had not so far contributed. He was clearly under some considerable obligation to the man who had not only gone out of his way to find these remarkable fishes, but had done everything possible to facilitate matters. Pearse had promptly sent them; had put his collecting privileges in Mexico in jeopardy; and had answered queries as quickly as humanly possible. However the cavalier attitude that Hubbs had shown towards the Mexican authorities sometimes extended to his academic colleagues.

This was October 1st 1936. The report on the caves of Yucatán did not go to press until 20 months later, in May 1938, and there is no doubt that it was a failure by Hubbs to complete and submit his contribution expeditiously that was the cause of much of the delay. Between October 1936 and November of the following year Pearse, always courteous but increasingly frustrated, sent a series of letters asking Hubbs about progress and pointing to the urgency. At times he was even close to pleading ("*Have a heart man, and finish up*"). He apparently gave up: there are no further letters from him after November 1937. The matter was turned over to the Smithsonian editorial staff and finally, after further delays due to Hubbs asking for last minute changes to text and tables, the report was published (G21B028; G27B028) (Hubbs 1938).

Hubbs was known for having numerous projects active at the same time in various stages of development, and other demands on his time had taken priority (Miller and Shor 1997, p. 375). Only one of these concerns us here. He initially put the Yucatán paper aside because of a totally new development. By a great coincidence yet another undescribed Mexican cavefish had unexpectedly fallen into his lap. The earliest it is mentioned in the archive is in a letter of 16th September 1936, so he had received it around the same time that he also got Pearse's collection or very shortly thereafter (16.9.1936 CLH to Charles Mohr: G29B028).

His response on receiving this new fish could not have been in sharper contrast to the way he was dealing with the Yucatán fishes. He immediately (and urgently this time) started work on a formal description, laying aside the latter. Abandoning his normal tendency to perfectionism in order to rush to publication, he based the description on a single type specimen; designated two live fish that were not even in his possession as paratypes, and illustrated it with the bare minimum necessary in a taxonomic work– a photograph of a live fish in an aquarium. The decision to use this rather than, as would be normal practice, an illustration of the described holotype may have been because the holotype showed an abnormality of the jaw apparently caused by an old injury.

The paper was in print within a few weeks of receipt of the preserved type specimen (Hubbs and Innes 1936). Described on the basis of lacking eyes and pigment, it was named as a new genus and species *Anoptichthys jordani*. This was typical for the period.

That he was ready to postpone work on the important Yucatán fishes, and at the same time risk, perhaps permanently, relationships with loyal colleagues shows the priority he attached to the new species. This episode throws considerable light on his attitude in later years to "his" new blind fish. A particularly telling indication of his somewhat narcissistic claim is a later statement "… *my recent discoveries of five new blind fishes in the caves and artesian waters of North America*" (Hubbs 1940, p. 203). In fact he had not, other than in the loosest sense possible, 'discovered' any of them.

Historical context

The discovery of "*Anoptichthys jordani*" was to prove a milestone in hypogean fish research, and by extension in biospeleology.

Romero (2001, p. 44) distinguished six phases in the history of hypogean fish research: (1) pre-Linnaean 1541–1742, (2) first discoveries and research 1805–1854, (3) American Neo-Lamarckism 1868–1919, (4) dominance of typological thinking 1921–1940, (5) American renaissance 1936–1960, and (6) philosophical conflict 1960–1990. Phase 4 is characterized by incremental discovery and description of new species/populations most of which were assigned generic status solely on the morphological (typological) basis that they lacked eyes and superficial pigmentation (Romero 2001, p. 59). As already touched upon, interest in invertebrate cave fauna in general in North America mirrored this pattern.

Although the discovery of new hypogean fishes continued elsewhere (except in Europe) American-born scientists doing field studies outside the United States and experimental work in American institutions initiated a renewed interest in the subject, mainly because aspects other than taxonomy and morphology began to be investigated. This renaissance period is characterized by more comprehensive studies that included ecology, physiology, and behavior. This was partly because of the discovery of "*A. jordani*" in 1936.

By 1936 only 16 species of blind cavefishes had been described (Romero 2001). None were characids, and except the still unpublished Yucatán forms that Hubbs was working up, only amblyopsids and the catfish *T. pattersoni* were known to occur in North America. Things started to change that year when the new cavefish that Hubbs was to describe was discovered in Mexico (San Luis de Potosí state, central Mexico) in an accessible cave known as La Cueva Chica ("The Little Cave"). The precise circumstances leading to this discovery are not reported in contemporary sources and remain unknown. We know that Señor Salvador Coronado, a young Mexican in charge of the Fish Culture Station at Almoloya del Río near Mexico City, entered the cave and reported the find. The discovery, made on or about 1st November 1936, was not fortuitous. His report, translated from the original Spanish by Hubbs, states "… *to see the little fishes for which we had come*" (Hubbs and Innes 1936 p. 2). Local people from a nearby village were using water from the cave pool where the fish were found (Breder 1942, pp. 8, 10) so presumably they were the original source of the information. What

is recorded is that he visited the cave more than once, caught a hundred fish and without delay live-shipped 75 of them to Charles Basil Jordan (1902–1989) proprietor of the Texas Aquaria Fish Company in Dallas, Texas.

Jordan was responsible for bringing to the market several new tropical fish species from Mexico (Hubbs and Innes 1936 p. 1). Coronado's action in quickly providing a commercial firm with so many specimens of a remarkable and unique discovery – three-quarters of the animals he had collected – has the hallmark of a well-established and trusted relationship. This implies that he was a regular collector of Mexican fishes on behalf of Jordan.

The abundance of these cavefish was unprecedented. After all, almost all vertebrate cave populations (except for bats) tend to be small. In addition to their abundance, Coronado found them easy to collect using an aquarium net to scoop the fish out of the water.

Jordan thought those blind and pinkish animals were a fascinating novelty. He was also impressed because all of them arrived in Texas alive and healthy: particularly significant for someone whose business was largely dependent on the ability of live fish to survive transportation (Romero 1986a). Unable to determine the species, Jordan sent some fish to William Thornton Innes (1874–1969), a well-known aquarist and aquarium writer and publisher. Strongly suspecting that he had a new species in his hands, Innes remitted in November 1936 specimens together with Jordan's notes to Hubbs. Unknown to Hubbs, one of his contemporaries, Charles Marcus Breder, Jr. (1897–1983), Assistant Director of the New York Zoological Society, had also received some of the fish, and in a letter, Breder wrote to Hubbs: "*From the letter to Dr. Turner, I note that you were describing a blind brotulid from Yucatán. It occurs to me to tell you that Miss LaMonte* [i.e. Francesca R. La Monte (1895–1982)] *and myself are describing a blind cave Characin from Texas. What do you think of that? We are quite excited. If you have heard about the thing, I would be glad to get any additional gossip you may have on it*" (G26B028: 14.12.1936).

If Hubbs' immediate response upon receiving the letter and specimen from Innes implies that he attached the utmost importance to this new fish, his apprehension on receiving Breder's letter that he might have been pre-empted must leave no doubt. He was quick to respond (G28B028; 16.12.1936). First, he corrected Breder by telling him the fish was from San Luis Potosí, Mexico, not Texas. Breder may have thought that the fish in question was from Texas because Jordan lived there. Hubbs continued to explain that he had received a specimen from Innes, who initially thought of publishing its description, to which Hubbs wanted to keep the priority of the description because: "*I have had very great interest in blind fishes and Middle American fishes.*" He said that the description was already in press and hoped that nobody else had beaten him on that, expressing fears that, in the past, that had happened. Afraid of losing the primacy of describing the species, he had rushed the manuscript with most unusual expediency. The date of publication, 17th December 1936, is a mere six or seven weeks after Coronado 'discovered' the fish. Many of Hubbs' papers show him delaying responding to correspondence, submitting manuscripts, and proofreading them.

Very courteously, Breder replied: "*It's all yours. About an hour after your letter got off, we heard from Jordan, with words that led me suspect (sic) you were doing something; consequently, we stopped then, pending hearing from you. It strikes me that this is a particularly interesting find, and we may try to do something with it here. I would like to know what your future plans are, if any, so we don't cross wires.*" (G26B028; 16.12.1936).

Hubbs followed up by telling Breder the scientific name given to the fish, that the publication date was "*today*" and that the publisher, Ann Arbor Press, was rushing it. There is no question that he wanted to make absolutely sure that he had priority over the description of what he thought was a remarkable new genus and species of cavefish. He continued by saying that he had no plans for further work on the fish beyond systematics and that Innes would soon publish a popularized version of this discovery (G26B028; 16.12.1936). Breder immediately replied: "*Just to keep the record straight: we labored under the impression here that the fish had not been distributed elsewhere, and it was not until after writing you that we got his (Jordan's) somewhat ambiguous note which caused us to stop our description*" (G25B028; 18.12.1936).

Breder sent Hubbs a copy of a letter he received from Innes dated 18.12.1936 in which Innes says: "*Dr. Hubbs has sent me a carbon (copy) of his letter to you of December 16th. There is one point in it which is not quite clear to me, and since I can get a reply from you, I am writing to ask you about it. This is how far has your work advance and is there any question at all about Hubbs having priority. You see, I am planning to publish an article in the forthcoming issue of THE AQUARIUM* (sic), *and in it I have left a blank space for the title and date from Hubbs' paper, which should have been out before this. Without being certain at this point, I would feel I must withhold publication for another month. (…) In any case, I could act more satisfactorily to myself if I knew your wishes and plans. As a matter of fact, I expected the Hubbs' paper to be printed within a few days of the then date, that I wrote Jordan saying that I thought it would be all right to send fishes to you and to Shedd, without danger of confusion in naming. Fowler wanted me (sic) to rush out a description about two weeks ago, but I thought this would be an impertinence on my part, especially as I learned next day that Hubbs was interested. I then sent my photographs to use in his paper, together with all information that I had. He has used my name only by courtesy.*" Henry Weed Fowler (1878–1965) was Curator of Fishes, Philadelphia Academy of Natural Sciences. By urging a rushed description he must have recognized the importance of the new fish, but it is unclear why he thought that Innes, who was a publisher not a taxonomist, might be able to do it.

Innes added a handwritten note at the top of the letter that says: "*Carl, althou (sic) the collector is obligated to keep specimens for the Mex. Govt' (sic), I do not think Breder's source of supply was from these. Jordan, after your paper was well underway to press, asked me if I thought it* [illegible] *to send to Battery Park and Shedd, I said yes Maybe I was rush (sic)*" (G25B028; 18.12.1936).

Although he had acted perfectly ethically, Breder was in damage control mode with a colleague and friend who was jealous of potentially losing priority over the discovery. The confusion had arisen because the businessman Jordan, likely unaware either of the especially great scientific potential of the find or of the fundamental importance of priority

in academia, did not inform either one about where he had distributed specimens. But Hubbs and Breder were just some of the ones involved in this confusing race for priority.

Hubbs and Innes described the new species as *Anoptichthys jordani* (Jordan's eyeless fish). As Hubbs put it himself, this was "*most surprising, by far subterranean fish belonging to the family Characidae, of which no blind representative has ever been seen before*" (Hubbs and Innes 1936).

A few days later, on 29.12.1936, C. Basil Jordan sent a telegram to Hubbs to thank him for "*favors accorded in your papers*" in an apparent reference to dedicating the fish's scientific name to him. Hubbs replied in a 2-full-page manuscript letter thanking him for sending four fish that arrived alive. He added some behavioral observations and mentioned that not all individuals look alike. He suggested that some may be the result of hybridization with the eyed relative "sardina" *Astyanax fasciatus* (G25B028; 31.12.1936). These preliminary observations would later become the source of many discussions on the evolution and taxonomic position of this blind cavefish.

The discovery of this new fish attracted the immediate attention of other researchers. For example, Alfred C. Weed (1881–1953), then Curator of Fishes at the FMNH in Chicago, wrote a letter on 5.1.1937 (G25B028) to Innes saying that he was astonished that "*… a fish of this group and closely related to the common* Astyanax fasciatus mexicanus *of southern Texas should get into an underground water system and then become blind. The Cichlids of the Cenotes of northern Guatemala and southern Yucatán which apparently also inhabit underground waters do not seem to show any signs of losing their eyesight.*"

This letter was addressed to Innes and not to Hubbs, who was not only the first author of the paper but also the true professional ichthyologist of the two and someone who had already described fishes from the cenotes. Perhaps Weed was unwilling to communicate with a man who had been dismissed for insubordination from his position as an Assistant Curator at the Field Museum (Norris 1974, p. 588). In any case, Innes provided the letter to Hubbs, and, as might be expected, there is no evidence that Hubbs ever wrote Weed on this issue. Yet, Innes did reply to Weed. In his 7.1.1937 (G25B028) letter he thanks Weed for his interest and gives him some behavioral information about the two captive individuals and why he thinks there is great potential for scientific studies.

Another observation would fuel the idea of the fish becoming an excellent subject for study. In a 10.1.1937 letter to Hubbs, Jordan confirms that he had successfully crossed the cavefish and the surface forms of the fish and that the resulting fish (F_1 generation) show intermediate features in terms of eye development (G25B026; 10.1.1937). After hearing this from Basil Jordan, Hubbs replies to him in a 25.1.1953 letter that the positive cross of the two forms is "*extremely exciting news*" and asks that if the result of that cross survives, he would like to examine the eyes of the preserved specimens (G25B028; 25.1.1953).

The news of the discovery started to attract attention from unexpected quarters. For example from Albert Moore Reese (1872–1965), a professor of zoology from West Virginia University who was working on venomous snakes and antidotes. Reese wrote Hubbs asking if someone was working on the anatomy of the sense organs of the fish (G25B028; 23.1.1937). Hubbs answers by postal card telling him that Breder is interested in doing so (G25B028; 27.1.1937).

By now, the scientific and aquarium communities were impressed about the fish Hubbs and Innes described, but also because so many individuals of several cavefish species in a single locality; the amblyopsids, by that time the best-known cavefish family, were not so abundant. Second, the fact that all 75 individuals had arrived in the U.S. alive and were easily kept in captivity said something about the potential of this species as a research subject (Innes 1937). Third, this cave characin did not grossly display the hyperdeveloped sensory organs quite common among other cave animals. Fourth, it only differs from its likely ancestor, *Astyanax fasciatus*, in lacking eyes and pigmentation. Fifth, initial crossings showed that Mendelian genetics studies of this fish and its presumed ancestor were feasible and promising in revealing some aspects of its evolutionary history.

This cave fish was so intriguing that in both Mexico and the U.S. a great deal of interest arose. So, a group from the Mexican "Escuela Nacional de Ciencias Biológicas" composed among others, by José Álvarez del Villar (1908–1986) and Osorio Tafall (1902–1990), began the exploration of the whole cave system for the area which, as time went by, would yield over 30 cave localities containing this fish.

The other center of interest was in New York City. Only three years after the publication of the description, Myron Gordon (1899–1959), a geneticist on the staff of the New York Zoological Society, visited the cave in which the fish had been discovered. There he collected more individuals which were brought back to New York. Gordon's interest in the fish resided in its lack of pigmentation; after all, fish pigmentation had been his subject of research since the beginning of his scientific career in the late 1920s.

The lack of another structure, eyes, became the interest of another New York-based scientist: Edward Bellamy Gresser (1898–1951). Gresser was a practicing physician and a professor of ophthalmology at New York University. He would use the laboratories of the New York Aquarium beginning in 1936 when first Mexican Cave Characin arrived.

Hubbs was clearly satisfied with the prize of naming and describing a major discovery and did no further direct work on it. He did follow up and exchange views and ideas with others, but it was Charles Breder who took the most active research interest in it (Atz 1968; Romero 1984).

The Aquarium cave expedition to Mexico

In 1939, in collaboration with Gresser, Breder took the initiative of organizing and leading an expedition to Mexico to undertake field studies, obtain enough ecological information for a cave habitat display for the Aquarium, to shoot a documentary to be presented at the 1941 annual meeting of the New York Zoological Society and, most importantly, to bring back enough fish to conduct extensive laboratory research.

In January 1940, he met with other scientists, in which the expedition, known as "The Aquarium Cave Expedition to Mexico," was organized. By March 11th of that year, the group was already in Ciudad Valles, near La Cueva Chica, the fish locality.

In addition to Breder and Gresser, the other members of the expedition were:

- Stanley Crittenden Ball (1885–1956), curator of Zoology at the Peabody Museum of Yale University.
- Marshall Bishop, assistant in Zoology also at Yale and an experienced fish collector.
- Ralph Friedman (1904–1979), an archeologist of the New York Zoological Society, expected to investigate any track of past human activity in the area.
- William Bridges (1901–1984), curator for publications for the Society since 1935.
- Sam Dunton (1912–1976), a professional natural historian and photographer, then working for the Aquarium.

In Mexico, they would be joined by the "discoverer" of the fish (Fig. 2), and by Ramón Aguilar, a local English-speaking native who worked for the Mexican Department of Fisheries.

Besides the fact that most expedition participants suffered from "tropical fevers" (possibly histoplasmosis) after the trip, the expedition was a complete success. The narrative of the expedition has been extensively told in several long articles by Bridges (e.g., 1940, 1954). In addition, the amount of knowledge produced after this and other contemporary field trips to that area has been impressive.

Between 1940 and 1954, Breder, sometimes co-authoring with his wife Priscilla Rasquin (an American Museum of Natural History ichthyologist) or Gresser, published

Figure 2. Charles Breder (right) with Salvador Coronado in La Cueva Chica plumbing the depth of Pool 1, the site of the first discovery of the cavefish. The photograph was taken during the 1940 N. Y. Aquarium Cave Expedition to Mexico (New York Zoological Society, courtesy of J.W. Atz).

17 papers (148 pages of dense scientific information) in which this fish was the principal research subject (e.g. Gresser and Breder 1940; Breder and Gresser 1941; Breder and Rasquin 1942). Most of the work concentrated on its behavior, particularly responses to light, chemicals, and social behavior (schooling and karyotypic). He also made the most valuable contributions to our knowledge of this fish's sensory organs (eyes and pineal gland), metabolism, ecology, genetics, and evolution. Based on his observations of the cave populations and because the cave and the surface forms freely interbred, he was the first who strongly suspected that the blind depigmented cave fish was nothing more than a remarkable locally-adapted population ("ecotype") of the surface species *Astyanax fasciatus mexicanus*, long before modern techniques such as electrophoresis and karyotypic analyses were fully developed (Romero 2001, pp. 63–64). By the 1970s genetic analyses had convinced most biologists that this was correct. Hubbs, however, was strongly opposed and remained so until the end of his life (Fig. 3).

Carl Hubbs on evolution and the origin of blind fishes

Throughout his career Carl Hubbs was a consistent supporter and advocate of Neo-Darwinian evolutionary theory, advancing a selectionist and adaptationist point of view. He referred to Darwin as "*the greatest biologist of all time*" (Hubbs 1941a, p. 74). He was unwavering in belief in the centrality of Darwinian natural selection in the process of speciation, and openly critical of those skeptics who doubted or rejected it as the main mechanism driving organic evolution. Although not being one of the "architects" of the Modern Evolutionary Synthesis (MES), his work has been credited with substantially contributing to its development during the first half of the twentieth century (Ilerbaig 2009). As a pioneer of mass-collecting methods and applied biometrics in studying natural variation, he contributed to the introduction of population thinking in evolution. Studies of variation and hybridization in fishes in the 1920s and 1930s contributed to understanding the problem of speciation and he used his many reviews of published works to advance his own views on the processes of speciation and evolution. Despite this, he never accepted the biological species concept which is considered a pillar of the MES.

Born in 1894, Carl Hubbs grew up and came of age in a seemingly unpromising social and intellectual environment for the incubation of a lifelong Neo-Darwinist. Much of the general population believed in a literal interpretation of the "Book of Genesis": evangelical protestant faiths had reached their heyday in the middle of the nineteenth century but remained a powerful presence in the religious landscape of the nation (Frankiel 1988). Within educated and academic circles acceptance of the antiquity of the earth and the fact of biological evolution was the norm by the turn of the century, but for the most part evolution was interpreted within a Neo-Lamarckian framework (Romero 2009, pp. 21 et seq) or as a progressive teleological process: "*God's way of doing things*". Darwinism, in the sense of evolution by natural selection, was viewed with considerable skepticism. As the prominent Congregational pastor, evolutionary theologian and author Lyman J. Abbott (1835–1922) put it: "*All biologists* [now] *accept evolution; practically, all natural scientists accept evolution ...*

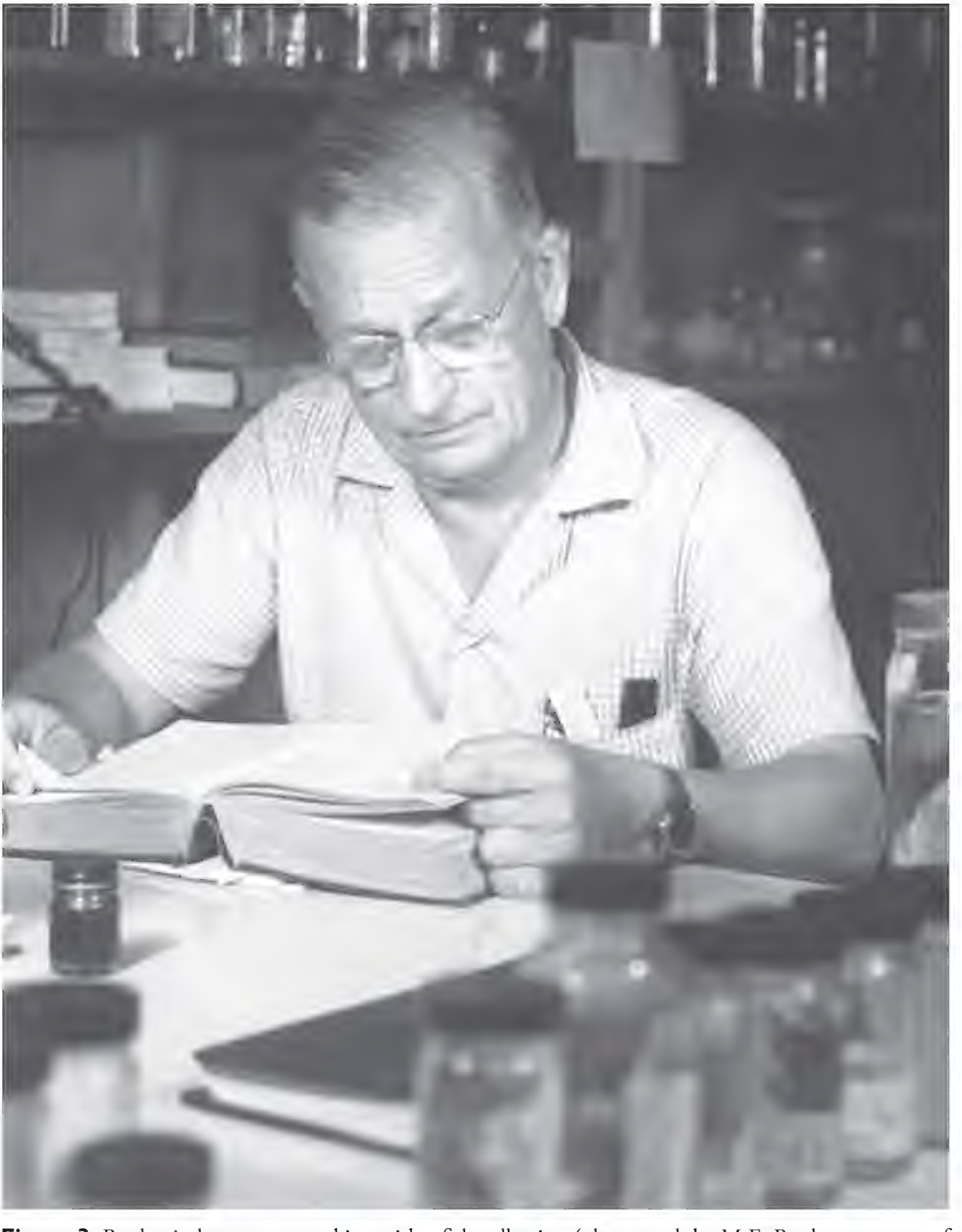

Figure 3. Breder, in later years, working with a fish collection (photograph by M.E. Braden, courtesy of Ms. P. Rasquin-Breder).

Evolution is to-day accepted as the clue in their investigations by all teachers, in all departments, in all colleges and institutions of learning, except possibly in the department of theology" … [but] … "*Darwinism is not evolution, though it is often in popular imagination confounded with evolution. Darwinism stands for the doctrine that the progress of life has*

been due to a struggle for existence in which the fittest have survived and the unfittest have perished" (Abbott 1897 pp. 95, 177). The first decades of Hubbs' career were during this period famously called "*the eclipse of Darwinism*" (Huxley 1942; Bowler 1988, 1992).

But Hubbs seems to have been unaffected: a story he told in a talk given at Scripps Institution in 1974 reveals that even at a young age he already accepted organic evolution as a fact of life. He recalled attempting when still a schoolboy to produce an illustrated phylogeny of the Mollusca (Shor et al. 1987, p. 219). The explanation of his independence of mind might be found in a free-thinking family who for example had sympathies with unconventional metaphysical religious movements. Objecting to the strictures of the public school system, his mother enrolled him in a private school run by Theosophists. He was there for three years.

Hubbs' early work on fishes focused on intra-specific variation through analysis of correlations between meristic variation, geographical distribution and physical conditions (Hubbs 1918, 1921a, 1921b, 1922, 1924). His doctoral dissertation reviewed this work; first deriving general conclusions and secondly drawing attention to some possible implications in evolution, speciation and phylogeny (Hubbs 1926b). He argued that these local morphological variations are best interpreted as the result of what he called adaptive physiological differences: "*The role of adaptation in evolution is probably more extensive than it has generally been held to be in recent years*" (p.69). However the ideas he expressed about evolutionary implications had little impact. Google Scholar (Accessed 25th May 2023) lists 178 citations of the paper. Most are in works on ontogenetic processes and phenotypic plasticity with very few citations in publications directly dealing with evolution.

He next turned his attention to a study that was to contribute his most significant and novel finding. Before going on to this, it is worth noting that the 1926 paper has a section dealing with the problem of "*degenerative evolution*" (pp. 70–72, 77). It does not mention blind fishes but may have a bearing on his later thinking about their evolution.

By 1930 Hubbs had begun a study of hybridization in fishes, work in which his wife Laura (1893–1988), a mathematician by training, fully collaborated. Their first co-authored paper was on their experimental demonstration of hybridization in sunfish, evidence for the existence of viable natural hybrids in fishes, a possibility previously disputed (Hubbs and Hubbs 1932). This was followed by demonstrations of the phenomenon in other species and even the existence in some cases of inter-generic hybrids.

The significance of hybridization in fish speciation and evolution was hardly recognized then. When "The New Systematics"(edited by Julian Huxley) appeared in 1940, Hubbs was mentioned only once, briefly. Recognition had to wait. A later comprehensive review of natural hybridization between fish species is by far his most cited publication (Hubbs 1955). Google Scholar (accessed 25th May 2023) reports 1151 citations. A search through these confirms that the significance of hybridization as an evolutionary mechanism in fishes is well recognized now.

Thus by 1940 Hubbs had had a major role in introducing population thinking into the study of organisms in nature, had begun to show how the results of such studies help reveal the mechanisms driving speciation and evolution, and in a collabo-

rative effort with his wife, had discovered what has proven to be a significant factor, natural hybridization.

In 1941 "The American Naturalist"added a new "Reviews and Comments"section. As its first editor Hubbs focused on reviews of publications dealing with evolution and on other items of interest to those working in that field: "*Emphasis is given to books and major articles which fall within the special scope of* THE AMERICAN NATURALIST *in that they deal with the factors of organic evolution.*" Until the journal "Evolution"appeared in 1947, "The American Naturalist" was a valuable forum for American biologists interested in the subject, and Hubbs took full advantage of the opportunity this offered him as an influential platform on which to promote his own views. Throughout the years of his editorship (1941–1947) he expressed those views in a series of reviews of published works. These reviews may well constitute his main contribution to the MES. In the absence of any monographic work, they offer picture of his thinking through the 1940s, the crucial period during which the MES was firming up and becoming established. It is generally considered to be complete by the end of the decade.

The review of Julian Huxley's "Evolution: the Modern Synthesis "is introduced with "*It would probably be no exaggeration to call this the outstanding evolutionary treatise of the decade, perhaps of the century. The approach is thoroughly scientific; the command of basic information amazing; the synthesis of disciplines masterly*" (Hubbs 1943a p. 364). The extent of agreement is emphasized by the fact that most of the review consists of text quoted *verbatim* from the book with explanatory introductory comments added. Selection and adaptation are central: "*Evolution is a joint product of mutation, recombination and selection*" "*Adaptation is omnipresent*". Lamarckian explanations are rejected: "*The Lamarckian interpretation is neither necessary nor tenable*" (Huxley [1942] quoted in Hubbs 1943a, pp. 365–366).

Hubbs is dismissive of those biologists who accept the truth of evolution yet contest Darwinian natural selection as the sole or primary mechanism. He was particularly critical of the saltationist theory espoused by the German-American geneticist Dr. Richard Goldschmidt (1878–1958) which he attacked in several reviews e.g. Hubbs (1941b, 1945). In reviewing Goldschmidt's 1940 book entitled The Material Basis of Evolution he is especially critical of the distinction made between microevolution and macroevolution (Hubbs 1941b).

The somewhat eccentric "Age and Area" theory proposed by botanist J. C. Willis was another target. Like Goldschmidt, Willis favoured saltational evolution. He questioned the adequacy of natural selection of small chance variations as the main mechanism, turning to "… *a compelling internal force 'differentiation (orthogenesis)' and regards it as 'a kind of compromise' between special creation and natural selection*" (Hubbs 1942, p. 96).

Turning now to his specific speculations on the evolutionary origins of blind fishes, we have seen how the roots of his keen interest can be found in the 1922 discovery of the Halfblind Goby when he was 26 years old. Eigenmann had already drawn attention to the similarities of behavior shown by the Blind Goby and other gobies occupying much the same habitat, and also its morphological similarity to cave fishes

(Eigenmann 1909, pp. 65–69). Discovery of *Lethops* enabled Hubbs to postulate an evolutionary pathway from a fully-eyed ancestor "pre-adapted" because of a comparable lifestyle. He was to adopt an analogous model to explain the origin of blind cave fishes. The concept of pre-adaptation can be challenged (Romero 2009 pp. 141 et seq.) but it does imply active colonization of subterranean habitats, which was by no means universally accepted in the 1920s.

The potential for active colonization by preadapted species was also implied in the case of two epigean fishes – a sculpin *Cottus b. bardii* and a minnow *Rhinichthys cataractus* – captured in Sinks Cave, Randolf County, West Virginia. These had been sent by Prof. A W Reese (West Virginia University) for identification. In his response (7.3.1933: G29B028) Hubbs commented that "*both species live largely in swift water under stones, so are logical candidates for cave inhabitants, and good material for cave speciation*".

The relative or total absence of predation afforded by caves is one factor probably involved in the process of active colonization. Hubbs proposed it to explain the large size reached by some individuals in a permanent or semi-permanent population of sculpin in an Indiana cave (see above). That was in 1924. There was another example which came to light much later as a result of the post-War revival of interest in cave fauna within the American caving community.

Hubbs had always followed up rumors and reports of possible new blind subterranean fishes (see above) and became very interested in such reports west of the Rockies. He was therefore immediately intrigued when in December 1953 Raymond deSassure of the Nevada-based Western Speleological Institute sent him a single, rather poorly preserved, specimen of a minnow collected by Jon Lindberg (the son of the famous aviator) in the "Daylight Zone" of Bower Cave, Mariopa County, California (1.9.1953: G30B29). The individual had lost all its pharyngeal teeth – a key diagnostic character in these fishes – but based on other features and geographical locality Hubbs tentatively assigned it to a common local species *Hesperoleucus symmetricus*. He was initially excited by the possibility that it represented a cave-adapted endemic subspecies: "*In that event, this would be the first differentiated cave fish to be discovered in the Pacific drainage*". This optimism was based on the rather thin evidence of its cave habitat, apparently isolated from surface waters, and the observation that the anal and dorsal fins each had one fin ray less than normal. Naturally, he asked if additional specimens might be collected for confirmation (CLH to deSassure 8.12.1953: G30B29).

Copies of his letter went to the collector, Lindberg, and, testifying to the potential importance of such a discovery, also to his close colleagues Wilbur Irving Follett (1901–1992), Curator of Ichthyology, California Academy of Science; Garth Ivor Murphy (1922–2001), a fisheries oceanographer at Scripps; Robert Rush Miller (1916–2003), a University of Michigan ichthyologist; and Phil Cummings Orr (1903–1991), Curator of Paleontology and Anthropology, Santa Barbara Museum of Natural History. There was also a direct request to Jon Lindberg for, if possible, the collection of further material (14.12.1953: G30B29).

In response, deSassure confirmed from personal knowledge that the cave lake was almost certainly completely isolated hydrologically, and that another, better specimen

of the minnow had already been collected some months earlier and sent to Dr. Follett. It was actually Follett who had originally identified Bower Cave as a possible site for cave fishes and three years earlier had examined it, initially with negative results (16.11.1950: Follett to Danby, G1B028). The site was attractive for exploration and Lindberg made an exploratory dive there using SCUBA equipment, finding an extensive underwater cave and capturing a single fish specimen (8.4.1953: Orr to Hubbs, G1B028). Follett's identification of this specimen as *H. symmetricus* confirmed Hubbs' preliminary opinion based on the new example collected during a second dive (17.12.1953: G30B29).

In the meantime Hubbs had had the opportunity to meet with Follett and together they had compared the cave specimen to examples of the local subspecies collected not far from the cave. They concurred that it did not differ in any substantive way. He conjectured that his specimen was merely an old individual that had lost its pharyngeal teeth with age (CLH to deSassure 21.12.1953: G30B29).

Despite this, Hubbs remained interested (further evidence that he saw all cave-collected fish including normally epigean forms as worth investigation), and asked Follett if deSassure could collect more specimens (CLH to Follett 21.12.1953: G30B29). DeSassure had already told the latter that only a few more might safely be taken because the isolated colony appeared to be small (deSassure to Follett 20.12.1953: G30B29). Interestingly it was *deSassure* who, in a reply to Hubbs' suggestion that his specimen was an unusually old individual, pointed out that, as the topography of the cave offered protection from predators it could have survived longer than usual for the species (9.1.1954: G30B29). Hubbs claimed to have already had the same idea (undated [1954]: G30B29).

There was an addendum to this exchange of letters when Jon Lindberg himself contacted Hubbs with further information about the collection site, and recommending against taking further specimens because very few fish had been seen (13.1.1954: G30B29). Hubbs replied with thanks and that must have been the end of the episode (27.1.1954: G30B29).

To return to the 1920s, Hubbs had speculated about the origins of the blind marine gobies but had yet to say anything specific on the evolution of cave fishes other than linking the unusually large size of cave-dwelling sculpin in Indiana caves with an absence of predators – an observation that has some relevance to the early stages of cave colonization. There is mention of so-called "degenerative evolution" in a speculative discussion of various aspects of fish evolution in relation to differential growth rates, but without direct reference to cave fishes. Presumably, no relevant data was available at the time (Hubbs 1926b). For the next decade he maintained an interest in cave fishes, collecting them whenever he had an opportunity and almost certainly in the unfulfilled hope of discovering new species. But it was not until the mid-1930s that material coming into his hands from others enabled him to begin to speculate seriously about their speciation and evolution.

The two fish species collected in Sink's Cave had been consistent with the hypothesis that blind cave fishes are descended from ancestors preadapted by lifestyle, and there was nothing about the catfishes taken in caves during the 1932 Yucatán expedition that might have challenged this interpretation. Populations of *Rhamdia guatemalensis*,

the common "bagres" catfish of the region, were present in cenotes and caves. Specimens from the open cenotes were unusually black; in contrast those collected in caves were partially depigmented with reduced but functional eyes. Based on relative body measurements and gill-raker counts, Hubbs – a notorious "splitter"- described the cave forms as new subspecies *Rhamdia g. decolor* and *R. g. stygia* (1936, pp. 201, 203).

The new Yucatán stygobites that Pearse collected in 1936 were already being worked up for publication when Hubbs received the specimen of the blind fish he was to name *Anoptichthys jordani*. This was a total surprise: a blind cave form living in proximity to an obvious immediate ancestral species which is not in any perceptible way preadapted for subterranean life. "*The discovery of this blind characin was most unexpected, for* Astyanax, *a free-swimming, midwater fish, does not possess the crevice seeking habits nor the well-developed sensory organs that are ordinarily characteristic of the ancestors of blind, subterranean fishes*" (Hubbs and Innes 1936, p. 3). Nothing like this had been found before. It was so remarkable that, as we have seen, other priority work was laid aside so that a taxonomic description could be rushed through to publication (Hubbs and Innes 1936).

The long-delayed paper on the new Yucatán blind cave fishes is the only inclusive treatment available covering Hubbs' views on the topic of blind fish evolution and speciation. In it he casts his net widely, listing all then-known blind forms (excluding deep-sea species). He describes the two new species and amends previous descriptive accounts of other relevant forms while also speculating on their evolutionary origins and those of blind fishes in general (Hubbs 1938).

"Pre-adaptation" had been a common thread since discovery of *Lethops*. Now in this paper he assembles and summarizes all the evidence which he has to support it as the fundamental concept underlying and explaining the evolutionary history of all blind fishes. All, that is, until now: "*Anoptichthys*" was an anomaly and hence a challenge. But it did not trigger any deep questioning or reappraisal of the concept. It was treated as an exception to the general rule resulting from a special situation. Nevertheless an admission that this "*circumstance indicates that almost any fresh-water fish may have the capacity to become a blind, unpigmented cave form, provided other conditions are favorable for this speciation*" suggests that Hubbs did have an inkling of a much broader issue (Hubbs 1938, p. 271).

The proposed model excludes more diverse colonization routes. It is proposed that caves and other dark habitats are actively colonized by species already moderately preadapted to life in darkness by their cryptozoic or nocturnal habits, typically already with some associated reduction of the eyes, and with tactile and other non-visual sense organs relatively well-developed. By "*moderately*" Hubbs means to exclude the idea sometimes proposed that "*fully*" preadapted blind species colonized caves. Emphasis is placed in this paper on evidence that sense organs such as the barbels of catfishes are necessary preadaptations. This was a new factor that Hubbs had not referred to in previous publications. Reproductive methods were also added and briefly addressed as possible useful or necessary preadaptations.

Only these moderately preadapted species are able to enter and establish viable permanent cave populations. It is worth reiterating here that despite the deficiencies of the

concept of preadaptation, it does at least constitute recognition that the colonization of caves is an active process. It tells against the idea that cave animals arise from accidental strays that became trapped or other such passive mechanisms. That Hubbs understood this point is demonstrated by his remark that "*The not infrequent finding of strays of free-living species in caves shows that caves are very frequently populated with a nucleus from which cave species could theoretically evolve. There is little ground for supposing, however, that mere accidental strays have become modified into cave types, for such strays would not likely have been common enough to have formed a breeding stock, or would not have found conditions suitable for reproduction*" (Hubbs 1938, pp. 270–271).

Speciation, a process Hubbs recognized as distinct from colonization, takes place "*within*" the subterranean environment. It is stated to be characterized by reduction and eventual loss of eyes, loss of dermal pigmentation, and enhancement of non-visual sensory organs. However, as will be documented below, it is clear that in practice it is the loss of eyes alone that is the factor that is used to differentiate a new species.

Turning to the mechanisms driving speciation, Hubbs overlooked the obvious role of natural selection in adaptive enhancement of sensory structures, and focused only on what he called "*degenerative evolution*". Rejecting the Lamarckian implications of "*use and disuse*" he considers the proposal that reduction of eyes and pigment confer a competitive advantage by conserving energy, but observes that can hardly be the case with endoparasites, which also lack eyes and pigment. The simplest explanation, he contends, is the survival of what he calls "*mutations of loss*" in the absence of strict natural selection (Hubbs 1938, pp. 270 et seq.). Passive genetic drift as an explanation of troglomorphic atrophy in cave animals had already been proposed by the late nineteenth century (Weismann 1885, 1889). Hubbs evidently was unfamiliar with the European biospeleological literature.

The species question

At the beginning Hubbs took it for granted that here was an entirely new form worthy of the status of a new genus. It was obviously very different in appearance from the related but well-pigmented open-water fish with fully-functional eyes. All the fish collected by Coronado were eyeless and almost completely depigmented, and Hubbs himself had virtually equated the process of speciation in cave fishes with reduction and loss of these two traits. Further, the La Cueva Chica population appeared to be ecologically isolated, potentially an important factor enabling speciation.

The genus "*Anoptichthys*" was described as differing from *Astyanax* only in characters associated with subterranean life, specifically eyelessness and depigmentation. The latter was downplayed: color being treated only as a species-specific character (Hubbs and Innes 1936, pp. 3–7). The genus was, therefore, based on a single, though apparently stable, morphological character i.e., lack of eyes.

Establishing a new genus solely on the basis of these traits was in no way unusual. It was common practice at the time. For example, a number of stygobiotic isopods had

been described as species of *Caecidota* on this basis, even though there was little doubt that they were independent lineages derived from multiple ancestral species of *Asellus* (Miller and Hoy 1939).

This of course reflects the prevailing typological species concept, which was not to be widely questioned until the early 1940s with adoption of the biological species concept by Mayr. In the case of blind cave animals, however, there is an additional factor that is usually overlooked: "[eyelessness and depigmentation] *are visually striking to us but the undue emphasis put on them is profoundly anthropocentric and has become ingrained. Witness use in the literature of scientifically meaningless adjectives such as "bizarre" to describe them. Absence of vision and of superficial pigmentation are hardly the most important features enabling an organism to survive in the lightless subterranean. Indeed, it was the fact that they seemed to him not to be in any way essential or even advantageous that so famously puzzled Darwin who, unable to see a "Darwinian" explanation resorted to the vague concept of disuse* (Darwin 1859, p. 137: and all subsequent editions)" (Moseley 2022, p. 40).

However, for some time Charles Breder had harbored doubts about the taxonomy of these fishes. The initial straightforward picture, that "*Anoptichthys jordani*" represented a local subterranean population which had evolved in isolation into a new blind species, had become unsustainable. It had been shown that in aquaria it was able to interbreed with the surface fish producing fertile offspring, and the Aquarium Expedition of 1940 found individuals in the original locality showing all stages of eye development. Then a second population of blind fishes had been discovered by the Mexican group in Los Sabinos Cave, which is approximately twenty-five kilometers north of La Cueva Chica. Fish collected here differed consistently though in relatively minor ways from "*jordani*": these differences are listed in a letter dated 14.10.1942 from Breder to Hubbs (G13B028). Hubbs' interpretation was in full conformity with the model expressed in his description of the Cueva Chica cave fish. He viewed the new fish as another isolated species, proposing to describe it as *Anoptichthys profundorum*. Breder had reservations. When invited to co-author the description he declined, citing his doubts in the 14.10.1942 letter. The relevant part of this letter is worth presenting at length: "*My feelings in regard to the taxonomic status of these things is* [sic] *still in a state of flux, confusion or what have you. The more I find out about them in the lab or otherwise the more flighty my notions become. It is this, of course, that has led to our metaphysical 'arguments'. You seem to have a definite view on the handling of such material … frankly I do not know yet whether I want to call this new form a species, subspecies or let it ride as a genetic phenotype … In the meantime I would rather not commit myself on paper. You may have noted that our various papers have all carefully skirted around the subject which manner of treatment stems from the same mental perturbation.*"

Nevertheless, he goes on to say that because "*profundorum*" differs in more characters from *A. jordani* than the latter does from *Asyanax*, designation as a full species might indeed be justified. He was much less conflicted about the relationship of *A. jordani* to the surface fish having already written a paper stating that the Cueva Chica "*cave characins show complete intergradations with the river characins … and surely represent a single population*" (Breder 1942, p. 14). The following year, he reported that

while the first (1936 and 1939) collections of the Cueva Chica fish consisted of only blind individuals, eyed forms had appeared by 1940, and the ratio of eyed to blind had increased by 1942 (Breder 1943b; Romero 1983). This evidence "*would seem to indicate that the blind fish* ***which have been called*** Anoptichthys jordani *by Hubbs and Innes were once separated genetically from the river population of* Astyanax mexicanus … *they have evidently been rejoined by the river population … when they were still able to interbreed freely …* [thus] … *the question of whether the intermediates should be looked upon as hybrids or merely genetic variations of the same stock would seem* [for now] *to be merely academic*" (Breder 1943a, p. 28). Conceivably intermingling "*has prevented the La Cueva Chica stock from* ***evolving into a form that could no longer interbreed with the river fish***" Breder (1943a, p. 30) (Current authors' bold).

In his reply to Breder's 14.10.1942 letter Hubbs does not respond or refer to the latter's concerns, asking instead that Breder reconsider co-authorship (17.10.1942: G13B028).

Sadoglu (1956) and Poulson (1964) supported interpretations comparable with Breder. Then Avise and Selander demonstrated that an analysis of genetic variation strongly supported the view that the subterranean Cueva Chica and surface populations are conspecific (1972, pp. 3, 16). Most biologists now accept this interpretation.

It was not, however, accepted by Carl Hubbs. Despite the increasing strength of the evidence, he remained entrenched in his original belief that they were distinct genera and species, allowing only that others might combine the genera, although he still preferred not to.

The Hubbs Archive is silent on the question of the conspecificy of *Anoptichthys jordani* and *Astyanax* until 1965 when an amateur ichthyologist called Michael Oliver wrote asking very sensible questions about it (29.10.1965: G16B29). Hubbs replied at length, clearly stating his position. Basing his argument on the observation that (so far as was known at the time) intermediates only occurred in the mouth of one cave (i.e. Cueva Chica) they were natural hybrids between the full cavernicolous species and *Astyanax*, which had later reinvaded the cave. It should be remembered in this connection that Hubbs had worked extensively on natural interspecific (and intergeneric) hybridization in fishes and would have found this easy to believe. With regard to whether generic separation was justified, he felt that because genus is an artificial concept, this was a matter of opinion, but he still himself favoured separation (16.11.1965: G16B29).

Shortly after receiving a copy of the Avise & Selander paper, Hubbs sent a very critical letter to John Avise stating that lumping the two species was a "*travesty on biology and commonsense*" and anyone who would do this "*needs a new pair of glasses*." The cave and surface fish are different "*kinds*" (his word) of animal, differing in structure, behavior, habitat and all. Interbreeding is not the only criterion. (20.11.1972:G11B29). Avise replied with a courteous letter pointing out that the results of biochemical investigations must be reported objectively without personal opinions or data based on such factors as morphology, ecology, or physiology (5.12.1972: G22B29). Although perhaps being too diplomatic to say so, Avise must have realized that Hubbs did not understand the

work, because his criticisms did not actually address the methodology or results. There was, for instance, no claim in the paper that interbreeding was a criterion for the claim of conspecificity.

It was also rather patronizingly suggested that Avise had been "*a little brainwashed by Mayr*". Evidently, even at this late date when it was becoming broadly accepted within biology, Hubbs rejected the biological species concept. His reasoning constitutes most of his review of Mayr's "Systematics and the Origin of Species"(Hubbs 1943c pp. 175 et seq.).

His position on the nature and taxonomy of the cave characins remained the same. He remained adamant that the surface fish, the Cueva Chica fish ("*Anoptichthys jordani*"), the Sabinos fish ("*Anoptichthys hubbsi*"), and a third population that had been discovered in another cave were distinct taxonomic entities (by which, of course, he implied species). In a 1973 letter to Dr. Jacques Gery, the world's top specialist in characids at the time) he makes this clear: "*I still think that the three types of* 'Anoptichthys' *are distinct entities, even though one of them hybridizes occasionally with* Astyanax fasciatus mexicanus *in one cave mouth!*" (10.9.1973: G10B29).

A letter sent to Basil Jordan, the man who had been so involved at the beginning, is the last mention of this topic in the archive. It makes a nice bookend to the story. Jordan had heard of the name change and wondered about it (21.8.1974: G11B028). Hubbs replied: "*I think that calling* Anoptichthys jordani Astyanax mexicanus *is a downright travesty, as they are certainly not the same kind of beast even if they do interbreed in aquariums, and in the mouth of the cave where the species was first found. There has been a tendency to put blind fishes and their ancestors in the same genus, and that is just a matter of opinion. I would prefer to see* Anoptichthys *retained.*" (29.8.1974: G11B028).

Conclusions

From the 1920s onwards, throughout the period referred to as 'the eclipse of Darwinism' and long before biospeleologists in America began to do so, Carl Hubbs was thinking about blind fauna within a Neo-Darwinian evolutionary conceptual framework. Although he had hoped to consolidate and publish his ideas, he never found the time and had little discernible impact on development of evolutionary biospeleology. In any case he worked in isolation, unfamiliar with the current trends and developments in cave biology taking place in Europe, and the general Neo-Lamarckian and teleological intellectual climate in both there and in the USA would likely not have been receptive at the time.

In a broad 'history of biology' context the case of Carl Hubbs and the description of new species of cavefishes represents an interesting case of conflict between personal prejudices and the emerging scientific consensus within the Neo-Darwinian movement. He was a lifelong advocate for Neo-Darwinism, for example, using his reviews in The American Naturalist in support while criticizing robustly those authors expressing alternative theories of evolution. Recognizing the need to adopt popula-

tion-based approaches he routinely used mass-collecting methods in fish taxonomy, and was a pioneer in demonstrating natural inter-specific hybridization in fishes. Although not being one of the recognized "architects" of the MES, his work has been credited with contributing to it. Puzzlingly, despite all this, he never accepted one of its most fundamental pillars, the population-based biological species concept.

His difficulty is well-exemplified by the case of the Mexican Cave Characin, a blind fish that was described with a colleague in 1936 as a new genus and species. When new findings began to show that it was merely an ecotype of a common, fully-eyed surface species, he was vehemently opposed, and remained so until the end of his life four decades later. Perhaps to some extent he took it as a personal affront, but it is illustrative of his deeper issue with the definition of a species.

There is no question that the description of this remarkable fish was, for Hubbs, a particularly notable achievement in his career as a classical taxonomist. It is for this reason understandable that he would be disturbed and resist seeing it 'downgraded' to little more than a local variety of a common widely-distributed species. This does not, however, explain his fundamental resistance to the biological species concept, of which this is only one, though very clear, example. In this regard, his use of the word "kind" to express his species viewpoint in the 1972 letter to John Avise is telling. It echoes pre-Darwinian fixism, showing that he still adhered to the views of many of his contemporaries that biological species represent separate distinct 'kinds' – analogous to periodic table chemical elements – and which led to the trenchant criticism of taxonomists as "glorified stamp collectors" as the physicist Lord Kelvin put it (quoted in Gould 2000).

Deeply aware as he was of variation within populations and of the breakdown of species boundaries through hybridization, he was nevertheless unable to take that small, but crucial, final step towards accepting the biological species. A consequence was that the taxonomy of "*Anoptichthys*" was fiercely contested by him not on its scientific merits but using metaphysical stances and personal criticism of colleagues who had come to a different conclusion.

This case represents an example of the truism that science is a human endeavor whose practitioners can have great difficulty in separating preconceptions and personal biases from the scientific consensus and the latest methodological approaches in the field. It is not only religious or social dogma that can hamper progress: the history of science has many examples of long-entrenched orthodoxies ultimately being swept away. As Carl Sagan (2011, p. 429) said, "*The cure for a fallacious argument is a better argument, not the suppression of ideas*".

Acknowledgments

We thank Scripps Institution of Oceanography Library for permitting the C.L. Hubbs Collection access; Brett Dion of The Wildlife Conservation Society who kindly made available photographs and the expedition film '*Blind Fishes of La Cueva Chica, 1942'* [WCS Film Collection, 5005. Wildlife Conservation Society Archives]; Steven Kerber of

Lovejoy Library of Southern Illinois University, Edwardsville, for providing access to materials of the Special Collections Department; Dr. Luis Espinasa made valuable comments as a reviewer of the original draft; James W. Atz for providing two of the photographs; Ms. Priscilla Rasquin-Breder for the photograph of her late husband; and Dr. Araceli Noguez Ortiz of the Universidad Autónoma de México for invaluable bibliographic assistance.

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